AERIFEROUS TISSUE IN WILLOW GALLS

A. Cosens and T. A. Sinclair

(WITH PLATES II–IV AND FIVE FIGURES)

Cosens (2) has demonstrated recently that in certain willow galls there is a production of aeriferous tissue in regions where it is not present normally. This investigation has been undertaken for the purpose of explaining the unexpected appearance of this tissue. Many different species of *Salix* and *Populus* were examined in order to determine the normal distribution of the tissue in their various organs. As an important adjunct of the work experiments have been conducted for the purpose of observing the influence of certain factors on its production, such, for example, as temperature, water, nutrient solutions, and light.

Stated in general, intercellular spaces are found in the parenchymatous tissues of nearly all plants. These usually remain small and inconspicuous, although connected with one another in such a way as to form a continuous gas-containing system of cavities. In many plants, however, especially hydrophytes, these spaces are so large and conspicuous and formed on such a regular plan as to impart the well known characteristic appearance to the areas in which they occur. Such a typical tissue is designated here aeriferous tissue.

Concerning the occurrence of this tissue in certain histological regions of *Salix* when under abnormal stimulation, two explanations present themselves: (1) that the tissue is an "environmental" modification, produced by the action of the plant protoplasm in direct response to certain conditions of the environment; (2) that the tissue is a distinct type, probably of wider distribution in the ancestral forms of the group, but now absent in certain regions of the modern species, since the power to produce it is dormant, but reinstated when these tissues are subjected to suitable stimulation. One example will suffice to illustrate the line along which attention has been directed. In many aquatic plants there are two types of leaves; for example, in *Proserpinaca palustris* L. the leaves on the submerged portions are divided, while those on the aerial portions are entire. Explanations, on experimental grounds, have been offered by various workers, notably McCallum, Burns, and Goebel, to account for this phenomenon of heterophylly.

McCallum (4) conducted a series of experiments with *Proserpinaca palustris* L., in which both submerged and aerial plants were grown under various degrees of illumination, and found that the type of leaf developed was entirely independent of the light relations. Further experiments were performed in which plants were kept in a perfectly saturated atmosphere containing normal amounts of carbon dioxide and oxygen, and it was observed that the water form of leaf persisted. It was then assumed that the essential factor common to moist air and water was inhibition of transpiration, and confirmatory experiments from this standpoint were carried out, in which transpiration was induced in submerged plants by high osmotic pressure. The conclusion arrived at was that the aerial type of leaf is developed, even under water, if sufficient moisture is withdrawn from the protoplasm.

From the preceding experiments the conclusion deduced was that the only factor, constant in all cases where the water form of leaf developed; was the checking of transpiration and constant increase in the amount of water in the protoplasm, while those chemical and physical conditions, resulting from partial withdrawal of water, are associated with the aerial type. The main point is that the modification in the form of the leaf was construed as environmental, that the form of the leaf is especially plastic under the influence of the transpiration factor.

Burns (1) studied the same plant and arrived at conclusions entirely different from those formed by McCallum. He experimented with cuttings and seedlings, and found that in the case of the former the disturbance of the vegetative activity caused a change that might be accompanied by a reversion, but concluded that environmental factors did not determine, in McCallum's sense, the type of leaf produced. A verification of this was obtained from the production of seedlings under varied conditions of light, temperature, moisture, etc. He also found in the case of plants grown from seed that the first leaves to appear were always divided, and that the entire leaves were of later growth. From further experiments he obtained the following data. All stems, regardless of external conditions, produced the water type in the autumn. Stems from which the vegetative points were removed in June threw out side branches with the water type of leaf, while normal plants under the same external conditions were producing the land type. In summer all plants, whether in water or air, developed the aerial form of leaf. Also, at the time of flowering only entire leaves were found. The change from the water to the land type took place earlier on strongly growing than on weak stems.

From his experimental results BURNS concluded that there are two forms of leaves, an adult and a juvenile, and that the production of these is not controlled by any one or more definite factors of the environment, such as light, moisture, temperature, etc. But under favorable vegetative conditions the adult form, the entire leaf, is produced, while under unfavorable the juvenile divided leaf is developed. Further, a reversion to the primitive or divided type may be associated with unsuitable vegetative conditions.

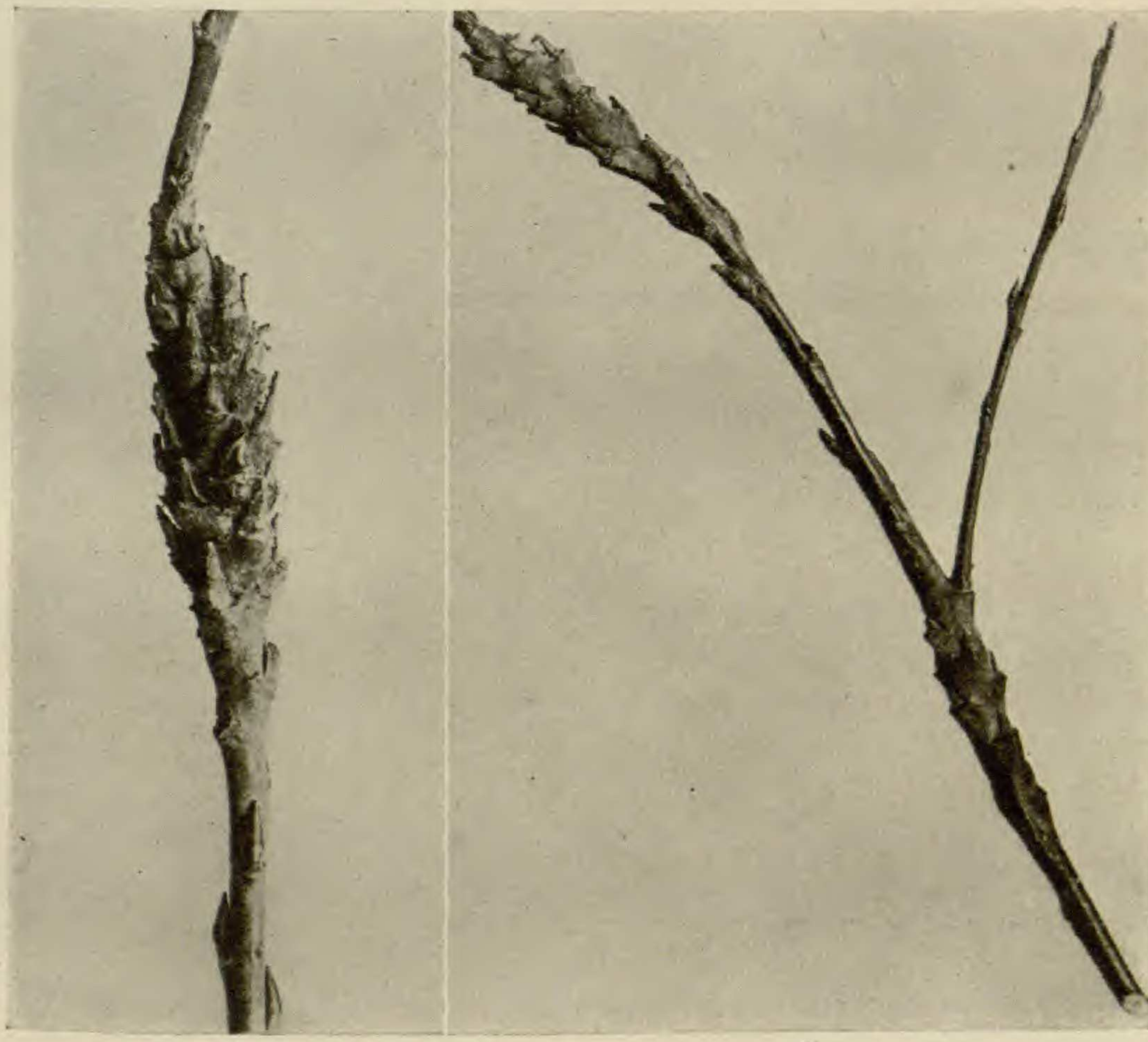
GOEBEL (3) experimented for several years with plants that exhibited the phenomenon of heterophylly, and his views fully confirm those of BURNS. He summarizes his conclusions concerning *Proserpinaca* as follows:

> Es ist klar, dass die Wasserumgebung nicht die Ursache der Blatteilung ist. Ebensowenig hängt sie ab vom Licht, der Temperatur, dem Gasgehalt des Wassers und dem Kontaktreiz als Solchem. Die einzige Folgerung, die sich aus meinen Versuchen ableiten lässt, scheint die zu sein, dass Proserpinaca palustris zwei Formen hat, eine "Folgeform" und eine "Jugendform." Unter guten vegetativen Bedingungen hat sie das Bestreben, die Folgeform mit den ganzen Blättern, Blüte und Frucht hervorzubringen, unter ungünstigen Vegetationsbedingungen hat die Pflanze das Bestreben, die Jugendform mit dem geteilten Blatt zu bilden.

In view of the satisfactory results obtained from investigations on such morphological features, it seems entirely reasonable to hope that the anatomical aberrations occurring in galls may be capable of explanation by pursuing similar lines of inquiry and by making use of the anatomical principles unfolded by SCOTT, JEFFREY, and others in recent years. Several of these aberrations have been studied by the senior author; in this paper that of aeriferous tissue only is dealt with in detail.

Distribution of aeriferous tissue in galls

Aeriferous tissue is abnormally present in galls produced by certain species of at least two distinct orders of insects. Thus it has



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FIGS. 1, 2.—Fig. 1, Gall of *Rhabdophaga triticoides* Walsh on *Salix cordata* Muhl.; fig. 2, Galls produced by *Rhabdophaga triticoides* Walsh.

been located in the dipterous galls *Rhabdophaga triticoides* Walsh and *R. strobiloides* Walsh, stem galls on *Salix cordata* Muhl., and *Phytophaga rigidae* O.S. on the stem of *Salix discolor* Muhl. It also occurs in the hymenopterous gall *Pontania pomum* Walsh, a leaf gall on *Salix cordata* Muhl.

The stem gall *Rhabdophaga triticoides* Walsh is usually terminal or nearly so (text fig. 1), but sometimes occurs at varying distances from the tip of the stem; two or three galls occasionally are spaced along a branch and separated by sections of normal stem, as shown in text fig. 2. The gall, especially when of the terminal type, bears a remote resemblance to a head of wheat. It is produced by a very marked shortening of the stem of the host, accompanied by a decided increase in its diameter. The contraction of the infected

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FIGS. 3, 4.—Fig. 3, Gall produced by *Rhabdophaga strobiloides* Walsh on *Salix cordata* Muhl.; fig. 4, Gall of *Phytophaga rigidae* O.S. on *Salix discolor* Muhl.

stem is so pronounced that the lateral buds, which would normally occupy 25–30 cm. of the stem, are crowded into a space of 4–5 cm. As the characteristic alignment of the lateral buds is approximately maintained on the abnormal part of the stem, there are 5 fairly well defined rows of buds on the gall. In each of these buds a larval chamber is located.

Practically the entire pith and the cortex of this gall are composed of aeriferous tissue. It is absent only immediately around the zonal areas of the larval chambers, and in these regions it can be seen to have been obliterated by compression. The tissue is of the most typically aeriferous type, consisting of polygonal spaces bounded by strands seldom more than one cell in width. The distribution and character of this tissue can be seen in figs. 1 and 2.

The gall *Rhabdophaga strobiloides* Walsh (text fig. 3) is invariably terminal, since the solitary larva occupies the tip of the growing point, and thus prevents any elongation of the stem past the infected area. The condensation of the stem axis that results is, in this case also, the chief gall-producing factor, the top-shaped mass of aborted leaves representing the normal leafage of nearly a meter of stem. The entire cortex of the receptacle of this gall is composed of aeriferous tissue. It commences to appear in the pith, immediately beneath the compact tissues of the gall zones, and extends to a considerable distance from the point of infection (fig. 4.)

FIG. 5.—Galls on *Salix cordata* Muhl. produced by *Pontania pomum* Walsh.

In contrast with the two preceding species, a marked condensation of the stem of the host does not enter into the production of the gall *Phytophaga rigidae* O.S. (text fig. 4). This is apparent from the normal spacing of the buds that persist on the exterior of the gall. The pith of the stem in this form is occupied by the larva of the producer, and only small areas of parenchyma remain outside of the protective sheath of the gall, but in these aeriferous tissue can be detected. The cortex, which is very thick, consists entirely of the same tissue (fig. 6). Aeriferous tissue is also developed far in excess of the normal in the cauline stelar gaps comprised within the gall. A section of such a stem gap is shown in fig. 3.

The normal occurrence of aeriferous tissue in the Salicales will be discussed in detail later, but it may be stated here that, while it occurs in the stem pith of the three galls just described, it is not present in the corresponding regions of normal *Salix*.

The well known spherical gall produced by the sawfly *Pontania pomum* Walsh on the leaves of *Salix cordata* Muhl. (text fig. 5) furnishes another example of aeriferous tissue in association with a gall-producing stimulus. In its earliest stages the gall consists of a singularly compact tissue (COSENS 2), but gradually the aeriferous characters become evident, until almost the entire mass of the adult gall consists of tissue which is thus differentiated. Fig. 5 is a typical section from such a mature gall.

Distribution of aeriferous tissue in normal plants

For the purpose of determining the distribution of this tissue in normal plants, the following species of Salicaceae were examined: *Salix fragilis* L., *S. cordata* Muhl., *S. discolor* Muhl., *S. humilis* Marsh., *S. longifolia* Muhl., *S. lucida* Muhl., *S. nigra* Marsh., *S. petiolaris* Sm., *S. purpurea* L., *S. rostrata* Richards, *S. serissima* Fernald, *Populus balsamifera* L., *P. deltoides* Marsh., *P. grandidentata* Michx., *P. nigra* L., *P. tremuloides* Michx.

CORTEX.—At first sight the cortex, both primary and secondary, of all these species appears to consist of a compact tissue, but on further examination a well defined aeriferous tissue was found in the primary cortex of every one. It can be seen in sections taken from the apex of the stem and for some distance back (fig. 10), but in older regions it is destroyed by compression. The amount formed varies somewhat in different species. Thus in *Salix nigra*, *S. cordata*, and *S. fragilis* the entire tissue forming the primary cortex is aeriferous; the meshes are relatively large, and the walls inclosing them are as a rule but a single cell in thickness. In *S. rostrata* and *S. petiolaris* it is especially well differentiated at the angles of the stem; at some levels it is confined to these regions.

Among the poplars the largest amount of this tissue is possibly to be found in *P. nigra* and *P. tremuloides*. In the former it is very pronounced, for the cortex is an entire lattice work of it, and the air spaces are large and bounded by strands that vary from one to three cells in width. The meshes in *P. tremuloides* are likewise regular and clearly defined, but they attain their greatest dimensions at the angles of the stem. *P. balsamifera* is peculiar in that they are most abundant and characteristic immediately around the leaf traces, especially in close approximation to the bundles. Indeed, at the nodal levels the entire cortex consists of aeriferous tissue. It is less apparent in *P. grandidentata* and *P. deltoides*, for, though present, it is not as abundant nor as regularly defined as in the other species. Incidentally it may be stated that wherever this tissue occurs in the cortex of the normal plant it is much more abundant and better developed in corresponding parts of stem galls. This also applies to *Salix*.

PITH.—The pith is distinctive and important. It has been noted that the pith in the galls cited is occupied by a very pronounced aeriferous tissue, but this is not the case with the normal pith of any species of willow except in the reproductive axis. In every species examined it is a compact tissue without any indication of other than small, ordinary, inconspicuous intercellular air spaces. The pith illustrated in figs. 8 or 10, for example (a normal pith), stands out in striking contrast to the pith of the gall of fig. 2. It is especially noteworthy that in the latter case the medullary and cortical tissues are identical, both in their conformation and in the size and shape of their cellular constituents, while in the normal, the cells of the pith are much larger and closely packed. The air spaces of the aeriferous tissue do not result as an indefinite elongation of the cells, as in certain oak-leaf galls, but are the result of cell divisions which follow a definite law with regard to their polarity. The compact normal pith and the open abnormal pith appear to be fundamentally different types on this basis and on the basis of the peculiarities in the distribution of the latter to be noted.

Fig. 7 is a photograph of a normal stem of *Populus balsamifera* taken from a new shoot, and it illustrates the difference manifested by *Populus* in comparison with *Salix*. In all poplars investigated the plan of organization of the pith is that of an aeriferous tissue, though lacking the regularity found in the cortex. Were it established, as some believe, that *Populus* is the more primitive genus, this phenomenon would be important in explaining the aeriferous tissue in the pith of the galls of *Salix*.

NODE.—We have been taught to regard the node as a conservative part of the stem, one in which discarded tissues may still persist, so that much interest attaches to an examination of this region. It is at the node more than elsewhere in the stem that the aeriferous tissue is most abundant and characteristic in both willows and poplars. Thus in *P. balsamifera* it is particularly abundant immediately around the leaf traces, especially in close approximation to the bundle. The branch gaps likewise are occupied by this tissue, in the case of *Salix* extending well into the pith (fig. 8). In stem galls, for example, *Phytophaga rigidae* O.S. on *Salix rostrata*, this feature is always very pronounced; but most significant of all, the pith at the bases of the branches is typical aeriferous tissue. Fig. 9 illustrates this feature clearly, and is interesting in comparison with fig. 10; both are from *Salix lucida*, the former from the base of a branch, the latter from an internode.

LEAF.—The petiole is sometimes a vestige carrier, so that it is of interest to note that aeriferous tissue has been located here in several species of *Salix* and *Populus*, for example, *Populus balsamifera*, *Salix humilis*, *S. fragilis*, and *S. cordata*. As a rule it is confined to the part of the petiole adjacent to the stem. Elsewhere the ground tissue is of the compact type. In the blade there is no indication of it, as the palisade layer and spongy parenchyma are of the ordinary type. Yet in the leaf gall *Pontania pomum* on *Salix cordata*, practically all of the ground tissue is aeriferous.

SEEDLINGS.—The seedlings of *Salix serissima* Fernald only were examined. These were obtained by sprouting the seeds in a moist chamber between layers of filter paper in an incubator, and then pricking the young seedlings into small fern pans. Different stages were examined, but in none was aeriferous tissue found in the pith. It is present in the cortex.

ROOT.—The roots of the Salicaceae are devoid of a pith. The primary cortex, however, was examined in the roots of seedling plants of *Salix serissima*, and in young roots of *Populus balsamifera* and *P. nigra*, and was found to consist in part of a well differentiated aeriferous tissue.

INFLORESCENCE.—No part of the plant is considered more important as a retainer of vestigial tissue than the reproductive axis. It is of especial interest to find, therefore, that aeriferous tissue is developed and often beautifully typical and abundant in the pith as well as in the cortex in the reproductive axes of all of the species of *Salix* and *Populus* that were investigated. This is especially noteworthy in the case of *Salix*, because here and at the bases of the branches alone is pith of this type to be found. Figs. 11, 12, 13, and 14 are photographs of the pith of sections cut from the catkins of *Salix purpurea*, *S. humilis*, and *S. cordata*. Figs. 11 and 12 are of *S. purpurea* at different stages of development, the former from a young catkin, the latter from a mature one. This tissue is sometimes more abundant and typical in the pith of the staminate catkin, but a striking similarity exists in the form and distribution of the tissue in the two catkins of the same species. An examination of both was made in the case of *Salix alba*, *S. lucida*, and *S. longifolia*. In *S. rostrata*, *S. cordata*, and *S. nigra*, the aeriferous tissue of the pith is more clearly defined than in the cortex, but is present in both. The reverse is true in *S. lucida*, while in *S. discolor* there is no greater development in the one region than the other. The pith in the catkin of *S. petiolaris* is peculiar because it consists of a large-meshed aeriferous tissue, and often there are but two or three large spaces bounded by slender lines of cells.

Influence of environment on occurrence of aeriferous tissue

For the purpose of ascertaining to what extent the production of aeriferous tissue in the Salicales is dependent on external factors, several experiments were conducted in the growing of plants under conditions in which certain components of the environment could be controlled. Cuttings from various species were grown in culture solutions, in water, some totally immersed, and in soil. The effect produced by the variation of the illumination and temperature was also noted in a number of species. The following list comprises the more important experiments.

LIGHT RELATIONS.—Cuttings from *Salix nigra* Marsh., *Populus nigra* L., *Populus balsamifera* L., and others were sprouted in pots of earth. In the conservatory some of these were placed in a situation to receive the maximum light, others in a more sheltered position, and finally several in a light-proof chamber. The only effect noted was in the case of the sprouts grown in the dark. In those experiments the stems produced were flattened, and the tissues, which were greatly compressed, contained many parenchyma cells of particularly large size, but no aeriferous tissue.

TEMPERATURE RELATIONS.—Cuttings were sprouted as in the preceding series, but the experiments were conducted at several different temperatures. With the exception of an increase in the rate of growth, tissue effects were not produced.

INHIBITION OF TRANSPIRATION.—Cuttings from various species of *Salix* and *Populus* were weighted down in tall cylinders containing water and allowed to sprout when completely submerged. Some of these cuttings were placed in bright sunlight and others in more shaded situations. Sections were taken from the newly produced shoots at different levels, as the growing point, the base of the sprout, near its origin from the main stem, and also from shoots that had just emerged from the water. In this series the most marked effect found was the flattening of the stems and the compression of the tissues proportional to the depth at which they were grown. In no case was there any increase in the amount of aeriferous tissue produced; indeed, in the sprouts produced on cuttings from *Salix nigra* Marsh., the tissue was entirely lacking.

CULTURE SOLUTIONS.—Cuttings were sprouted in various nutrient solutions, including all of the formulae recommended by MACDOUGAL (5), and the results were checked by shoots produced in ordinary water. In the sprouts produced on *Salix* cuttings in nutrient solutions aeriferous tissue was not developed in the pith. While it was invariably present in the pith of the *Populus* shoots, it was not increased in amount beyond the normal production.

The results of all the experiments seem to justify the conclusion that the stimulus to the development of aeriferous tissue in the Salicales is not involved in light, in temperature relations, in the nutrient conditions imposed by the conditions of our experiments, or in checking of transpiration.

Discussion

As already stated, two theories present themselves in explanation of the unexpected appearance of aeriferous tissue in certain regions of insect galls where it is normally absent. The tissue may be regarded as a direct effect of the action of certain environmental factors on the protoplasm of the host; or it may be considered a hereditary tissue that has been reinstated owing to the awakening of latent characteristics in the protoplasm of the infected plant, on account of unusual conditions associated with the presence of the gall producer.

Concerning the alteration by experiment of the environment of the host plant, all attempts were unsuccessful either to increase the amount of aeriferous tissue normally present or to cause its development in regions where it is not found under normal conditions. Although the inhibition of transpiration is commonly regarded as an important factor in the production of this tissue, it was not increased to the smallest extent in the *Salix* sprouts developed under conditions of reduced transpiration. Indeed, if these experiments had given positive results, it would still be necessary to show that the conditions presented by galls are those of restricted transpiration. This is clearly not the case in *Rhabdophaga triticoides* Walsh, the gall in which the development of the tissue is the most pronounced and its characteristics the most typical. As stated previously, the lateral buds that contain the larval producers of this gall are situated on a length of stem, the internodes of which are shortened to a very marked degree. The occupation of the buds by the larvae, however, has not checked the development of the leaves in the axils of which the buds are produced. The galls shown in text figs. 1 and 2 were collected after the leaves had fallen. This results in the leaf area of the abnormal part of the stem being increased far beyond the normal leafage, a condition that we can scarcely associate with reduced transpiration. Thus the direct evidence from experiments leads us to believe that environmental factors of light, temperature, moisture, etc., are not directly operative in the production of aeriferous tissue.

The anatomical structure of the normal stems of the Salicales strongly favors the same view by furnishing facts apparently explainable only on the supposition that we are here dealing with a true heritable tissue. In accordance with the general view concerning the retention of ancestral characteristics, certain regions of plants are regarded as more tenacious of these structures than others. For example, it is commonly recognized that they may persist in the reproductive axes, petioles, leaf or branch traces, and roots. The tissue under consideration must be regarded as primitive in accordance with this general principle. It occurs in the pith and cortex of the reproductive axes of all species of *Populus* and *Salix*. It is found in the pith at the bases of the branches of the stem of *Populus* and *Salix*, and only in that region in the case of the latter genus. Further evidence in support of the same view is furnished by its presence in the branch gaps, its occurrence in petioles and the vicinity of stem and leaf traces, and in the cortex of the root. This prominent development of the tissue in the vestigial carriers of both *Populus* and *Salix*, taken in conjunction with our experimental results, presents strong evidence in favor of the theory that the aeriferous tissue in the Salicales is of ancestral type.

The power of the gall stimulus to arouse latent properties in the protoplasm of the host, expressed by its ability to produce an aeriferous tissue not normally present in *Salix*, is also exemplified in the case of glandular tissue and trichomes in certain galls on other plants. It may be stated as a general principle that glands, when they are present normally in a tissue of the host, are always more plentiful or larger in the gall originating from that tissue. A striking example (COSENS 2) of this is furnished by the pithy spherical stem gall produced on *Solidago canadensis* L. by *Eurosta solidaginis* Fitch. But in some cases glands are produced in galls on parts of the host normally glandless. Thus, they are plentiful in the stem gall *Neolasioptera perfoliata* Felt on *Eupatorium perfoliatum* L., but are not present in the same location in the normal plant. In fact, they were found in normal plants in the transitional region between stem and root only, both in this species and in *E. urticaefolium* Reichard.

Trichomes exemplify the same principle. When the gall produces unusual trichomes, the abnormal forms can almost invariably be found on the reproductive axes of the host. Thus, while the normal hairs on the leaf of *Quercus macrocarpa* Michx. are of the stellate type, those of the reproductive axes are acicular, corresponding exactly to those composing the pubescence of the leaf gall *Eriophyes querci* Garman on this host. Also, the convoluted type of hair present on the *Acarina* dimple gall on the leaves of *Acer Negundo* L. are exactly reproduced by the form occurring on the reproductive axes, although the normal leaf hair is straight.

An almost dormant characteristic has also been aroused in *Rosa blanda* Ait. by the cynipid producer *Rhodites multispinosus* Gillette (COSENS 2). The gall produced is always exceedingly spiny, although the stem of the host from which it originates is usually unarmed. But it is worthy of note that the production of spines is a marked character of other species of the genus. Doubtless further investigations will show that examples of this kind can be almost indefinitely multiplied.

The reinstatement in a gall of vestigial characteristics of the plant has an important bearing on the question of gall formation. The producer has long been recognized as exercising a directive control over the activities of the protoplasm of the host, but these examples of the rehabilitation of dormant characters show that the forces operative in gall formation are of wider scope. Under these conditions unexpected structures and unusual combinations may well be produced, and in the interpretation of the morphology of any gall it becomes necessary to discriminate carefully between these two classes of organs and tissues, that is, between those that are simply environmental modifications of the normal and those that are vestigial or in use in other parts only of the plant. Incidentally it may be added that there remains no authentic instance of any organ or tissue in a gall that is new, ontogenetically or phylogenetically, to the host.

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EXPLANATION OF PLATES II–IV

PLATE II

FIG. 1.—*Rhabdophaga triticoides* Walsh on stem of *Salix cordata* Muhl.: transverse section showing general arrangement of larval chambers and distribution of aeriferous tissue throughout the cortex and pith of the gall; ×10.

FIG. 2.—*Rhabdophaga triticoides* Walsh on stem of *Salix cordata* Muhl.: transverse section in which is shown the typical character of the aeriferous tissue produced under the stimulus of the gall producer; ×50.

FIG. 3.—*Phytophaga rigidae* O.S. on *Salix discolor* Muhl.: a stem gap which shows aeriferous tissue produced in excess of normal amount; ×90.

FIG. 4.—*Rhabdophaga strobiloides* Walsh on stem of *Salix cordata* Muhl.: a longitudinal section showing aeriferous tissue produced in pith of gall axis; ×25.

PLATE III

FIG. 5.—*Pontania pomum* Walsh on *Salix cordata* Muhl.: section of a nearly full-grown gall in which aeriferous tissue is produced throughout its mass; ×18.

FIG. 6.—*Phytophaga rigidae* O.S. on *Salix discolor* Muhl.: gall chamber includes all the pith area of the stem; aeriferous tissue of the characteristic type occupies whole of cortical region of the gall; ×10.

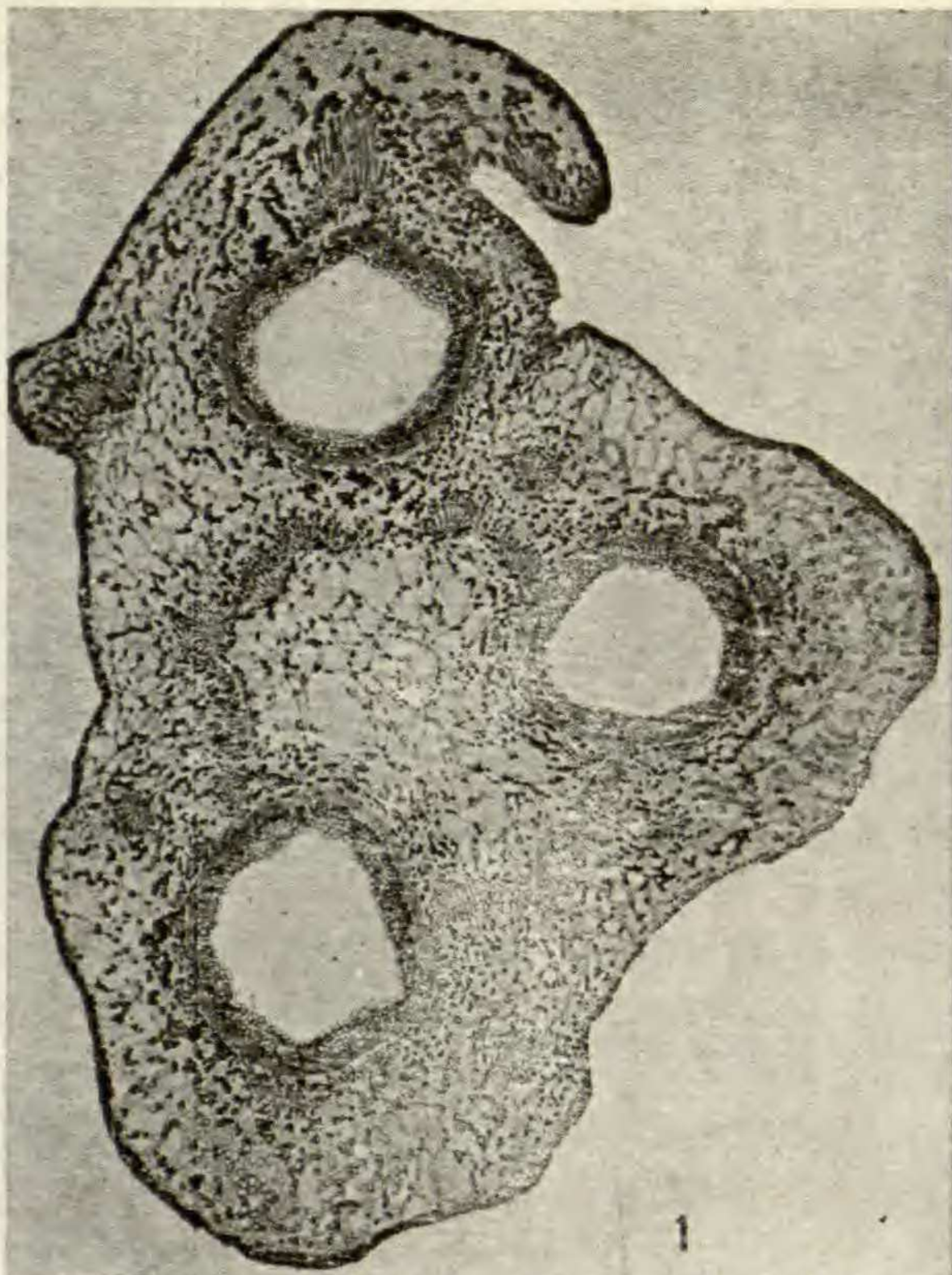
FIG. 7.—*Populus balsamifera* L.: transverse section of stem pith in which aeriferous tissue is normally present; ×80.

FIG. 8.—*Salix humilis* Marsh.: section of normal stem at level of a stem gap; it illustrates the compact nature of the *Salix* pith and the differentiation of aeriferous tissue in the stem gaps; ×65.

PLATE IV

FIG. 9.—*Salix lucida* Muhl.: section through base of a normal stem, showing aeriferous tissue produced in the pith; ×60.

FIG. 10.—*Salix lucida* Muhl.: transverse section of normal stem a short distance behind the growing point; aeriferous tissue constitutes the entire cortex, but is completely absent from the pith; this compact nature of the pith is typical for all species of *Salix* except in region of bases of branches as illustrated in preceding figure; ×12.



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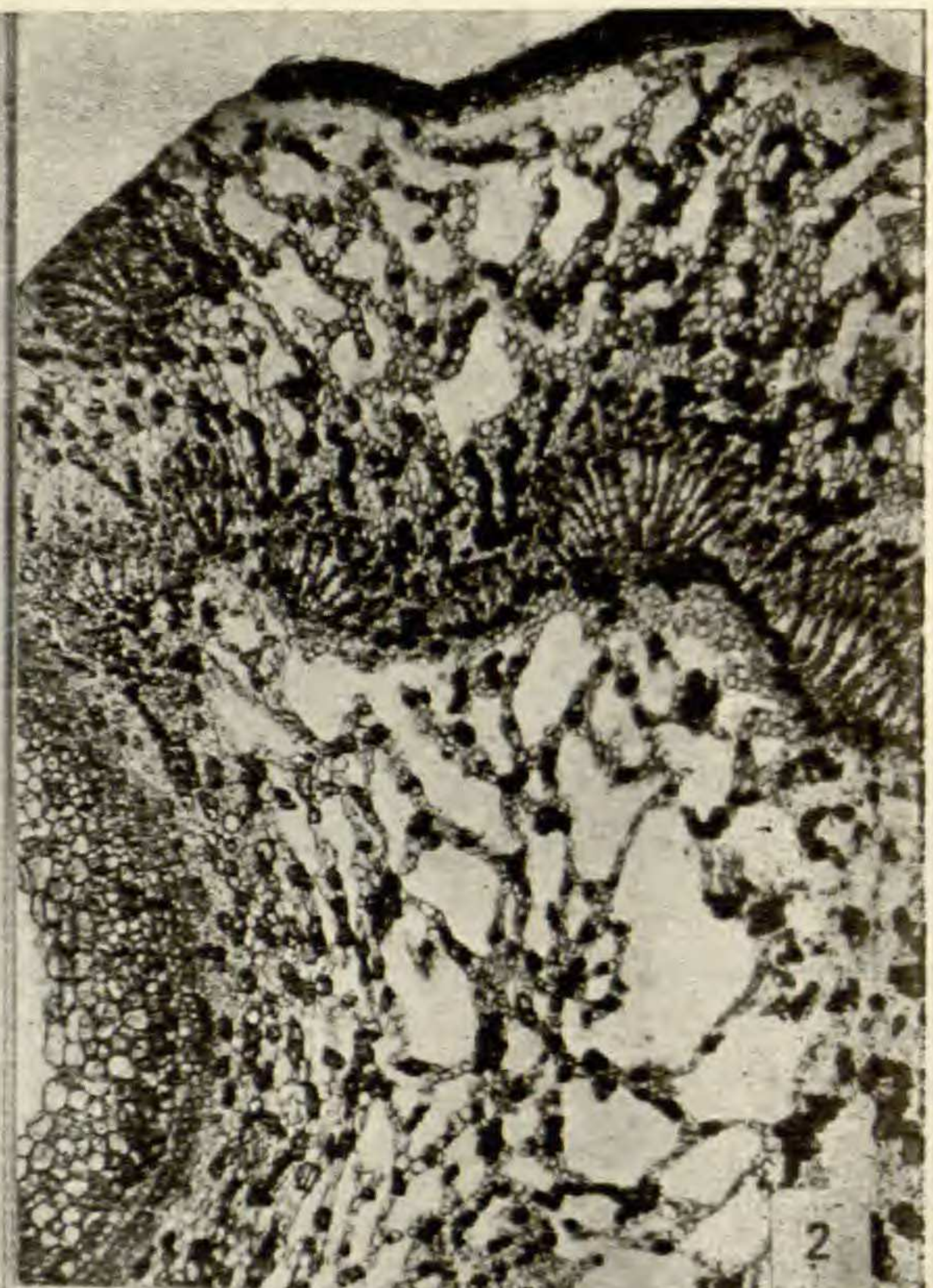

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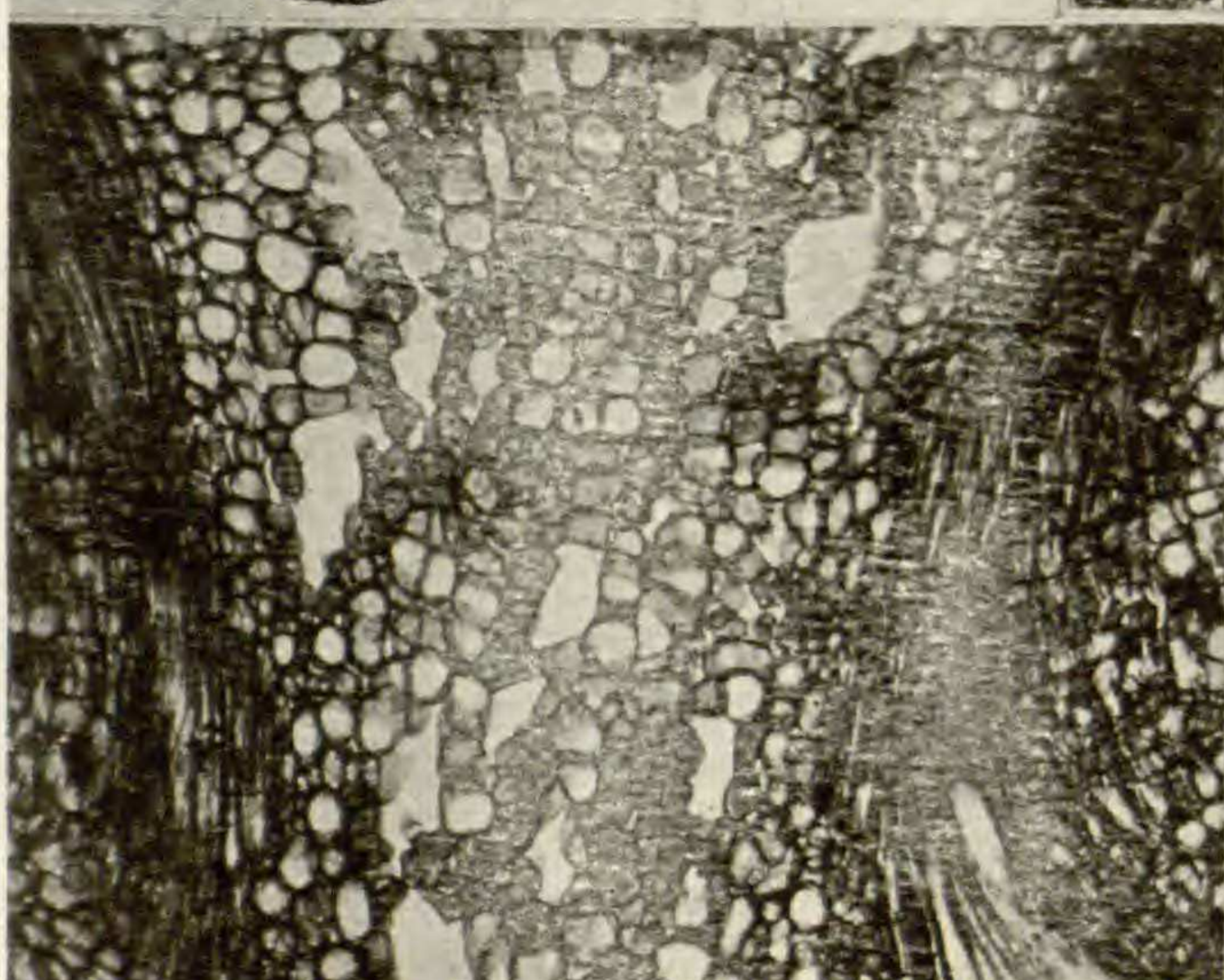

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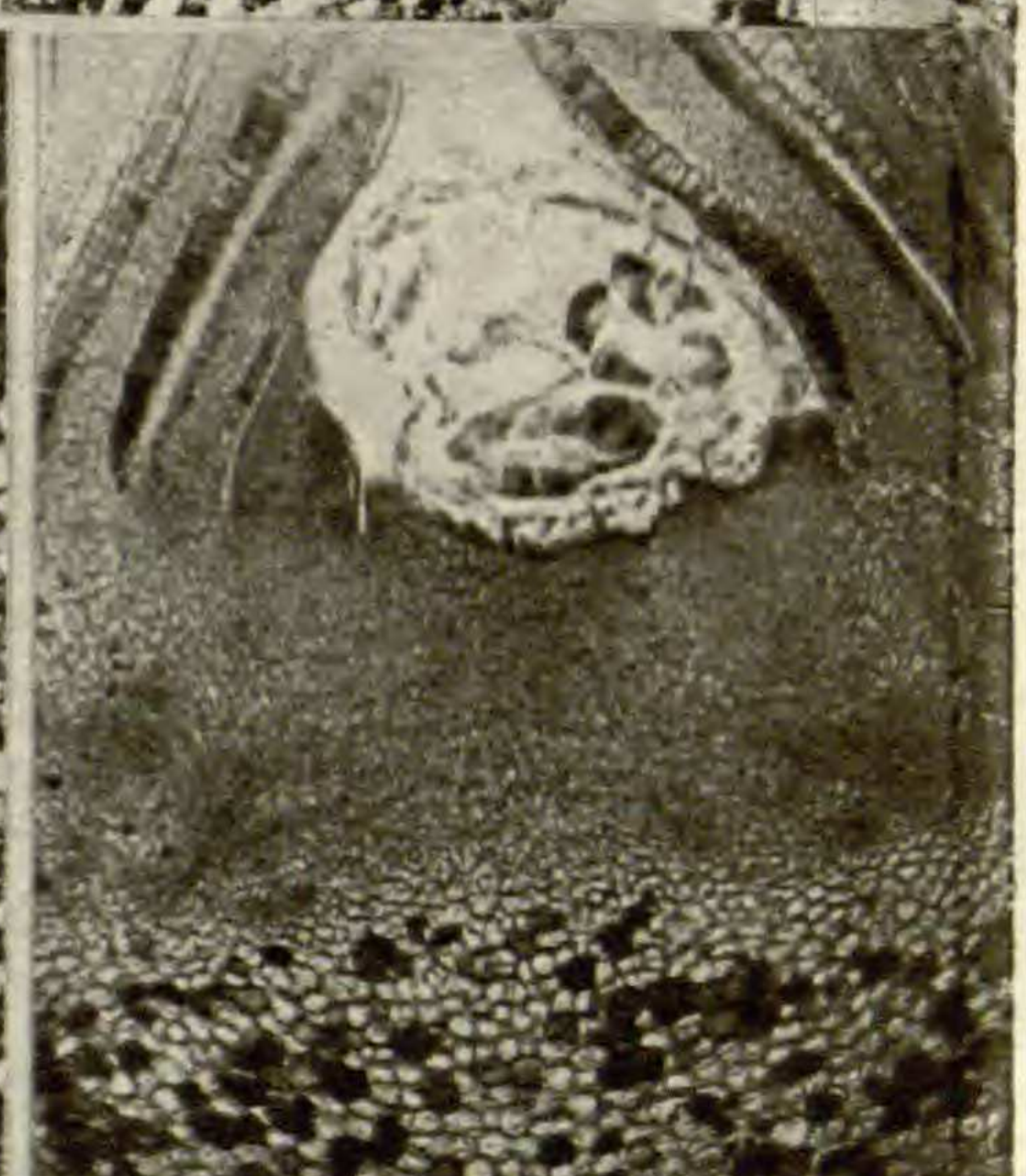

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COSENS and SINCLAIR on AERIFEROUS TISSUE